



# Endemism in host–parasite interactions among island populations of an endangered species

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## ABSTRACT

**Aim** Implicit in conserving interactions is the idea that species behave differently throughout their range, resulting in functionally dissimilar populations of the same species. Host–parasite interactions are a useful system to explore the pervasiveness of these ecological phenotypes. Here, we investigated whether the role of an endangered, endemic species to provide habitat for ectoparasites varies throughout the geographic distribution of the host.

**Location** Channel Islands, California.

**Methods** We captured island foxes (*Urocyon littoralis* sp.) from three populations: Santa Catalina ( $n = 72$ ), Santa Rosa ( $n = 79$ ) and San Miguel ( $n = 83$ ). We compared the extent to which variation in parasite attributes were due to differences among individuals or populations. As a measure of the latter, we used discriminant function analysis to determine whether individuals from the same population ‘cluster’ together when comparing patterns of intensity in various ectoparasites.

**Results** We identified eight ectoparasite species that included at least six new parasite records for island foxes. We found that ectoparasite attributes including diversity and intensity varied among host populations. More importantly, we show that knowing the parasite composition of the host can identify its population of origin, due to unique host–parasite interactions. Overall, we correctly ‘assigned’ 72% of island foxes to their actual, respective populations, although there were inconsistencies among populations.

**Main conclusions** If foxes generally have the same parasite assemblage regardless of their respective populations, then conservation of a single population likely maintains all necessary species interactions and discriminant function analysis is uninformative in discerning population assignments of individuals. Our findings highlight the importance of conserving populations to maintain endemic interactions and caution against extrapolating the ecology (i.e. known species associations) of a species to other locations within their range.

## Keywords

aggregation, assignment test, diversity, fox, isolation, parasite, prevalence, *Urocyon littoralis*.

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## INTRODUCTION

‘The history of evolution and biodiversity is fundamentally a history of the evolution of species interactions’  
(Thompson, 1999).

A growing body of work argues that conservation should target not only genotypes, populations, species and habitats,

but also interactions (Thompson, 1996; Forup *et al.*, 2008; Tylianakis *et al.*, 2010). Implicit in conserving interactions is the idea that species behave differently throughout their geographic distribution resulting in unique associations throughout space (Schemske *et al.*, 2009; Sexton *et al.*, 2009). Emphasizing species interactions also means that populations of a given species are not necessarily functionally equivalent. As such, efforts that consider not just the unique genes or

traits of species within populations, but also their unique interactions are needed to ensure the persistence of processes that promote species evolution, population viability and ecosystem health. However, a key barrier to conserving interaction diversity (i.e. the number of species associations within a specific locale or for a focal species of interest) is actually documenting whether distinct interactions among populations, especially isolated populations, exist.

Parasites by virtue of their diversity and dependence on other species are embedded within every ecological network or food web (Lafferty *et al.*, 2008), and therefore, parasite–host interactions are the most ubiquitous species interactions in nature (Poulin & Morand, 2005). Parasites account for most species on Earth (May, 1988), can exert strong selection pressures on their hosts (e.g. Wegner *et al.*, 2003) and can vary in their diversity independent of the number of available hosts (e.g. Krasnov *et al.*, 2004). On the one hand, extrinsic conditions such as the composition of alternative hosts or climate may cause the parasite assemblages of a host to exhibit marked differences across populations. Variation among populations is perhaps most prominent when one considers the parasite assemblage of a host species in its native versus introduced range (Torchin & Mitchell, 2004). Parasites may also be absent from or limited in host populations because competitive interactions and parasite-induced immune responses in the host that exclude certain parasite species from co-occurring (Pedersen & Fenton, 2007; Jolles *et al.*, 2008). This highlights the importance of considering host–parasite interactions in the context of local and regional environments.

On the other hand, one might expect that in at least some host populations, the interaction diversity between host and parasite is geographically invariant. For example, similar parasite communities and hence interactions may plague host populations throughout the range of species because of strong co-evolutionary histories or due to the persistence of common threats (Thompson, 1999). Arguably, the most fundamental resource delimiting distributions for parasites is the presence of hosts. However, which and how many hosts are present will affect the spatial patterns of parasite diversity differently. Numerous studies have demonstrated that where there are more host species there are proportionately more parasites (Novotny *et al.*, 2006; Harris & Dunn, 2010). This variation in parasite diversity across space also likely leads to variations in host–parasite interactions among host populations. Yet, while it is clear that interactions should be conserved, the extent to which these interactions vary among different populations of species in a predictably unique manner is less understood. We argue that understanding these differences in host–parasite interactions across the geographic distribution in a host is necessary to anticipate selective pressures and inform conservation priorities.

Empirical studies demonstrating the variation of host–parasite associations across host populations have been documented in few vertebrate systems (e.g. Poulin *et al.*, 2011), but such empirical evidence is plentiful for other types of interactions. For example, ruby-throated hummingbirds (*Archilochus colubris*) vary spatially and temporally in their contribution to pollination in a ubiquitous North American plant (Fenster & Dudash, 2001).

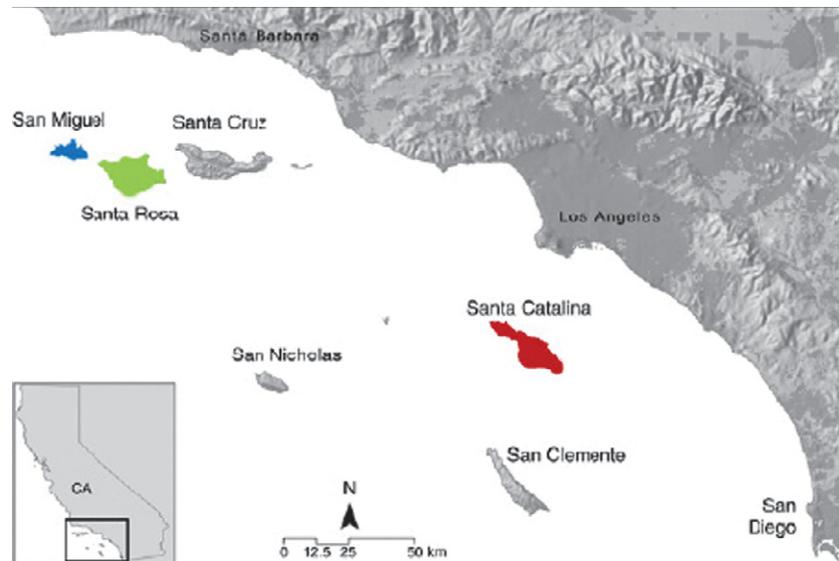
Considering predators and their prey, Canada lynx (*Lynx canadensis*) have a diet restricted to snowshoe hares (*Lepus americanus*) throughout most of its range, but populations in areas with high prey diversity exploit alternative species (Roth *et al.*, 2007). Here, we focus on the endangered island fox (*Urocyon littoralis* sp.), which resides only on the Channel Islands off the coast of California, to evaluate differences in host–parasite interactions across three populations. If populations differ in attributes, then the unit of interest for conservation should be the population, not simply the species; an argument recently made for island spotted skunks (*Spilogale gracilis amphiala*) due to their genetic variation among populations (Floyd *et al.*, 2011). Hosts already represent figurative ‘islands’ of suitable habitat with individuals acting as hierarchical replicates for parasites. Studying parasites on geographic islands further strengthens these among-population comparisons because islands literally are discrete locations with limited mammalian species turnover, which allow for various mechanisms influencing distributions to be isolated. Additionally, our study illuminates whether species of conservation concern exhibit expected associations with their remaining parasites, because often rare or geographically restricted species have fewer specialist affiliates (Altizer *et al.*, 2007; Harris & Dunn, 2010).

Specifically, we assessed whether individual island foxes differed in the composition, diversity and intensity of infection in the ectoparasite species they harboured. If foxes generally have the same parasite assemblage regardless of their respective populations, then conservation of a single population likely maintains all necessary species interactions. Next, we assessed how parasite intensity (i.e. load) was distributed among host individuals and determined whether this aggregation is a species-specific trait or independently defined within each population. Finally, we compared the extent to which variation in parasite attributes were due to differences among individuals or populations. As a measure of the latter, we determined whether individuals from the same population ‘cluster’ together when comparing patterns of intensity in various ectoparasites. If so, this would indicate the presence of unique host–parasite interactions that warrant additional conservation attention.

## METHODS

### Ectoparasite collection

Island foxes are a small endemic fox of the Channel Islands in California (Fig. 1), closely related to the larger bodied, widely distributed grey fox (*Urocyon cinereoargenteus*) on the mainland. Island foxes inhabit the six largest Channel Islands and diverged from the mainland species 10,000–15,000 years ago (Wayne *et al.*, 1991). Island foxes are listed as endangered due to disease and the colonization of a novel predator by the US Fish & Wildlife Service in four of those populations, excluding San Clemente and San Nicholas Islands (Roemer *et al.*, 2002; Coonan *et al.*, 2010). We captured and sampled individuals from three endangered populations in August–October 2009: Santa Catalina Island (SCAT; 33°24' N, 118°24' W), Santa Rosa Island (SRI; 33°57' N, 120°06' W) and San Miguel Island (SMI; 33°02' N, 120°18' W). SCAT



**Figure 1** Channel Islands. Shaded islands include populations from which island foxes were sampled for ectoparasites during this study: San Miguel, Santa Rosa and Santa Catalina Islands. Map modified from Bakker & Doak (2009).

(194 km<sup>2</sup>) located 32 km from the mainland has a resident human population *c.* 3200 residents, contains several mammals including exotic elk (*Cervus elaphus*), bison (*Bison bison*) and black rat (*Rattus rattus*). SRI (217 km<sup>2</sup>) contains exotic elk, deer (*Odocoileus hemionus*) and, an additional native carnivore, the island spotted skunk. SMI (37 km<sup>2</sup>) is the smallest of all the Channel Islands with only one other native mammal present, *Peromyscus maniculatus*. Annual average precipitation ranged from 32 to 42 cm across the three islands (Moody, 2000; Orrock *et al.*, 2011).

Island foxes were captured during annual trapping efforts to monitor population recovery led by the Channel Islands National Park and Catalina Island Conservancy. Once an individual was restrained, we systematically combed (*c.* 20 strokes) the entire body of the individual to collect ectoparasites using a flea comb. Ticks that are attached or engorged are unlikely to be removed through combing and, instead, were individually removed using fine-tip tweezers. This sampling method took *c.* 2 min, and ectoparasites were preserved in 95% ethanol for subsequent identification using pictorial keys and direct comparison with reference entomological specimens in museum collections.

### Ectoparasite summary statistics

We estimated prevalence and intensity of infection for each ectoparasite found during the sampling of island foxes. We calculated prevalence and the 95% confidence intervals as the number of individuals infected divided by the total number of individuals examined (Rozsa *et al.*, 2000). We used chi-square and 2-sample *t*-tests to explore differences in prevalence among island fox populations. We also calculated ectoparasite intensity as the number of ectoparasite individuals recorded from infected hosts; mean values with 95% confidence intervals are provided. We used multivariate analysis of variance (MANOVA) to evaluate whether the variation in intensity and diversity was due mainly to differences among

individuals or among populations for each ectoparasite species. Significant results indicated that among population, variation is larger than the variation among individuals within a population.

### Structure in ectoparasite communities

Key to understanding how parasites are distributed both within and among populations is knowing their relative abundance on different hosts. Disease theory and previous empirical studies have demonstrated a skewed, over-dispersed pattern in parasite intensity among individuals within a population; most individuals have few parasites, and only a small fraction of the population are heavily parasitized (Shaw & Dobson, 1995). But, if the population of interest has a greater proportion of susceptible individuals, deviations from the negative binomial distribution may exist. In addition, aggregation could either be consistent among populations (if it is an attribute of parasite species) or vary from island to island (if it is a function of local conditions). We evaluated the skewness of parasite distributions for each parasite species among populations using three common indices: variance-to-mean ratio, exponent *k* of the negative binomial and index of discrepancy (*D*). In aggregated populations, the ratio of the variance to the mean number of parasites per host is greater than unity and *k* approaches zero, while *D* tends towards a maximum of 1 (Poulin, 1993).

### Host population designation by ectoparasite assemblage

Individual hosts may differ in their susceptibility to parasites due to variation in their genotypes, behaviour, health, sex or other traits (Pedersen & Fenton, 2007; Jolles *et al.*, 2008). Or, hosts may differ not due to individual traits, but, instead, due to regional conditions. We used discriminant

function analysis to classify individuals from three island fox populations based on their parasite assemblages and used the leave-one-out cross-validation approach. This approach is robust to violations of normality and equal covariance assumptions, and only individual foxes with at least one ectoparasite were included in this analysis. Discriminant function analysis uses a priori information on group designation to minimize within group variance and maximize between group variance. We recognize that to develop conservation priorities, it is necessary to determine not only which parasites are present on an individual, but also which parasites are absent from populations. Using this rationale, one might in the future be able to determine the source population of a host individual of unknown origin solely by determining what parasites they harbour – representing a novel assignment test.

## RESULTS

### Variation in ectoparasite diversity among island fox populations

We captured 234 island foxes across three island fox populations (Fig. 1): Santa Catalina (SCAT:  $n = 72$ ), Santa Rosa (SRI:  $n = 79$ ) and SMI ( $n = 83$ ). The proportion of individuals infected with at least one ectoparasite species was high and the same (94% of individuals) on both SRI and SCAT. In contrast, less than a third (24/83) of island foxes was infected with any ectoparasites on SMI, the island with the fewest number of available hosts. Ectoparasite diversity also

varied among populations ( $F = 14.26$ , d.f. = 2,  $P < 0.001$ ) ranging from only two species on SMI to seven species on SRI (Table 1).

### Variation in ectoparasite prevalence and structure among island fox populations

When combining all ectoparasite species, overall prevalence ( $\chi^2 = 77.65$ , d.f. = 2,  $P < 0.001$ ) and mean intensity of infection ( $F = 3.79$ , d.f. = 2,  $P = 0.025$ ) differed among island fox populations, with the greatest prevalence and intensity of infection on SRI both overall and for half of all parasite species individually (Table 1). Nevertheless, in all populations, there was only one ectoparasite species that had prevalence levels that exceeded 50%. Differences in intensity among populations were observed for five of the nine ectoparasite species reported from island foxes: *Pulex* sp. (flea: MANOVA: Wilk's  $\lambda$ :  $F_{2,152} = 33.17$ ,  $P < 0.001$ ), *Ixodes pacificus* (tick:  $F_{2,152} = 7.69$ ,  $P = 0.001$ ), *Echidnophaga gallinacea* (flea:  $F_{2,152} = 5.42$ ,  $P = 0.005$ ), *Opisodasys nesiotus* (flea:  $F_{2,152} = 5.54$ ,  $P = 0.005$ ) and *Neotrichodectes mephitidis* (louse:  $F_{2,152} = 2.74$ ,  $P = 0.068$ ). Though, one might expect the intensity of parasite infection to be higher when fewer individual hosts are infected; overall, we found no association between prevalence and mean intensity ( $R^2 = 0.057$ ,  $P = 0.649$ ). *Ixodes pacificus*, the western black-legged tick, was the only species for which a parasite with low prevalence had a high mean intensity of infection when it was present (the case on SCAT, but not on SRI). The prevalence and infection intensity of *I. pacificus* has great

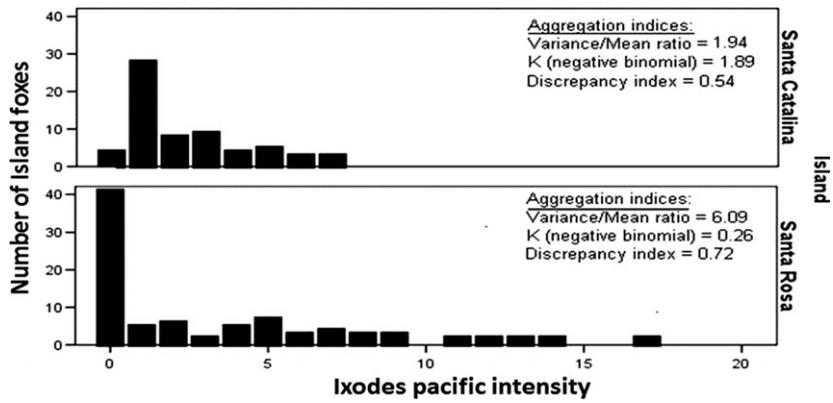
**Table 1** Summary statistics for ectoparasite species detected on three endangered island fox populations

| Parasite species                    | San Miguel Island                   |                       | Santa Rosa Island      |                       | Santa Catalina Island  |                       |
|-------------------------------------|-------------------------------------|-----------------------|------------------------|-----------------------|------------------------|-----------------------|
|                                     | Prevalence <sup>1</sup><br>(95% CI) | Mean load<br>(95% CI) | Prevalence<br>(95% CI) | Mean load<br>(95% CI) | Prevalence<br>(95% CI) | Mean load<br>(95% CI) |
| Louse                               |                                     |                       |                        |                       |                        |                       |
| <i>Neotrichodectes mephitidis</i> * | 0.27 (0.18–0.37)                    | 6.32 (4.55–8.50)      | 0.01 (0.01–0.07)       | n.a.                  | 0.31 (0.21–0.43)       | 18.82 (5.64–64.82)    |
| Flea                                |                                     |                       |                        |                       |                        |                       |
| <i>Opisodasys nesiotus</i> *        | 0.02 (0.00–0.08)                    | n.a.                  |                        |                       |                        |                       |
| <i>Pulex</i> sp.*                   |                                     |                       | 0.92 (0.84–0.97)       | 16.92 (13.49–21.38)   | 0.01 (0.00–0.07)       | n.a.                  |
| <i>Malareus telchinum</i>           |                                     |                       | 0.05 (0.02–0.12)       | n.a.                  | 0.01 (0.00–0.07)       | n.a.                  |
| <i>Echidnophaga gallinacea</i> *    |                                     |                       | 0.15 (0.09–0.25)       | 3.83 (2.67–5.25)      |                        |                       |
| <i>Oropsylla montana</i>            |                                     |                       |                        |                       | 0.01 (0.00–0.07)       | n.a.                  |
| Tick                                |                                     |                       |                        |                       |                        |                       |
| <i>Ixodes pacificus</i> *           |                                     |                       | 0.43 (0.32–0.54)       | 5.79 (4.59–7.21)      | 0.74 (0.63–0.83)       | 2.32 (1.91–2.81)      |
| <i>Ixodes kingi</i>                 |                                     |                       | 0.01 (0.00–0.07)       | n.a.                  |                        |                       |
| <i>Ixodes rugosus</i>               |                                     |                       | 0.05 (0.02–0.13)       | n.a.                  |                        |                       |
| Overall*                            | 0.29 (0.20–0.40)                    | 5.88 (4.21–8.00)      | 0.92 (0.84–0.97)       | 20.38 (16.14–25.56)   | 0.76 (0.65–0.85)       | 9.82 (4.42–28.15)     |

<sup>1</sup>Prevalence is the proportion of individuals infected of the total number of individuals sampled. Mean intensity (or load) is the average number of parasite individuals sampled on infected hosts. Shaded boxes indicate no ectoparasite of that species was detected, and n.a. indicates insufficient sample sizes to calculate population attributes.

\*Significant differences among island fox populations ( $P = 0.000$ ) in prevalence and mean intensity using chi-square test and multivariate analysis of variance, respectively.

**Figure 2** Distributions of ectoparasite intensity measured as the total number for the tick, *Ixodes pacificus* per infected host individual among island fox populations. *I. pacificus* was not detected on island foxes sampled from San Miguel Island. Three aggregation indices were calculated. High variance/mean ratios, *k* values close to 0 and *D* values close to 1 indicated aggregation.



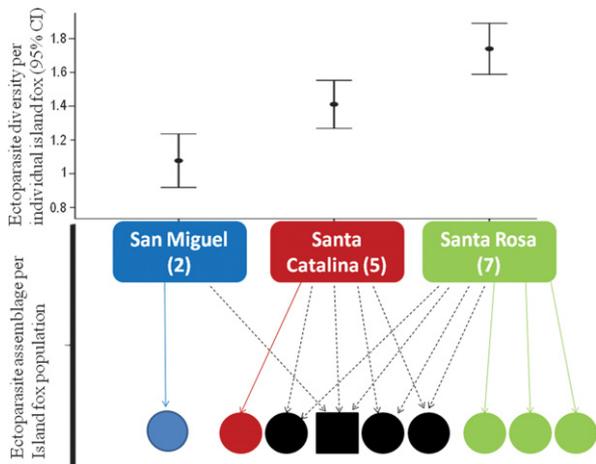
significance because this species vectors numerous zoonotic pathogens including *Borrelia burgdorferi* and *Anaplasma phagocytophilum*.

For all ectoparasite species that occurred in more than one population, the intensity of infection varied differently among individuals within a host population. In other words, the distribution of ectoparasite infection was not consistent among populations, indicating that intensity is likely not an intrinsic, biological attribute of the parasite, but instead a manifestation of extrinsic conditions. Most notably, *I. pacificus* was not detected on SMI, aggregated on SCAT, and more segregated in infected foxes on SRI (Fig. 2). Similar patterns in the lack of repeatability of aggregation metrics were observed when considering different ectoparasites. When we considered the mean intensity of all ectoparasites combined, all populations were structured (Discrepancy index: SCAT – 0.80, SRI – 0.55, SMI – 0.83).

**Unique host–parasite associations within island fox populations**

Five of the nine ectoparasite species were restricted to a single island, resulting in unique species interactions between parasites and host in each island fox population (Fig. 3). The fleas, *Oropsylla montana* and *Opisodasys nesiotus*, were only observed in association with foxes on SCAT and SMI, respectively. Differences among islands were not due simply to geographic distances among populations or to the mainland. For example, ectoparasite assemblages appear most dissimilar between SRI and SMI, despite their close proximity (c. 5 km).

A discriminant function analysis was used to test whether the population of origin for island fox individuals can be discerned based on the intensity and composition of their ectoparasite assemblage. The five ectoparasites that demonstrated greater among, than within, population variation were used in designating population assignments in the discriminant function analysis (Table 1). From this analysis, we found three distinct clusters, representing the populations sampled with SRI having the most within-population variation. The cross-validated classification showed that overall 72% of fox individuals were correctly classified to their actual population of origin, but there were inconsistencies among islands. Nearly all foxes (66/67) from the SCAT population were correctly assigned based on their ectoparasite composition, and correct assignments were marginal for foxes from the SRI population (51/74). In contrast, false assignments were highest from individuals occurring on SMI; 92% of these foxes were incorrectly classified as residing on SCAT. The two individuals from the SMI population that were correctly classified hosted only one ectoparasite affiliate, which represented a unique association.



**Figure 3** Variation in ectoparasite diversity and assemblage among island fox populations. Number in parenthesis is the total number of ectoparasite species reported. Black circles represent species present on more than one population. Colour circles indicate unique host–parasite interactions corresponding to the respective coloured island fox populations. The black square represents the only ectoparasite species found in all three island fox populations, the louse *Neotrichodectes mephitidis*.

**DISCUSSION**

Parasites are interesting and important in their own right, but have also become an increasingly visible tool for understanding hosts. Parasites have proven useful in understanding the evolutionary and biogeographic history of hosts, be they humans or hawks, across a range of temporal and

spatial scales (e.g. Reed *et al.*, 2007). In some cases, parasites can determine whether a particular host species is present, as for parasites that require multiple hosts to complete their life cycles (e.g. Byers *et al.*, 2011). We add to this growing list of examples of how parasites inform host's ecology by showing that knowing the parasite composition of a host individual can aid in identifying its population of origin because of unique host–parasite interactions. But we also recognize our conclusions from the discriminate function analysis are contingent upon the presence of unique host–parasite interactions. For populations with distinct parasite assemblages such as foxes on SCAT, discriminate function analysis can easily discern the correct assignment. However, false negatives (i.e. incorrect assignment to the host population) can occur when host populations harbour too similar parasite assemblages as was the case for foxes on SMI compared with those on SCAT.

### Variation in ectoparasite attributes among island fox populations

We demonstrated that host–parasite associations exhibited spatial variation among populations of an endangered host. Specifically, we found that island foxes on SRI had the highest ectoparasite diversity, but only shared one (of their 8) species in common with foxes on the neighbouring SMI.

In addition to the variation among island fox populations in the species composition of parasites, we also observed variation among populations in the attributes of the parasites. We found different levels of aggregation, intensity and prevalence in each ectoparasite considered among island fox populations. All island fox populations exhibited aggregation of varying degrees with a highly aggregated population on SCAT possibly indicating variation in intra-population susceptibility. Similar (and more extreme) levels of spatial variations in parasite attributes have also been reported in many other systems. For example, the mean number (i.e. intensity) of *Colpocephalum turbinatum* found in Galapagos birds ranged from 24 to 206 lice per individual across island populations (Santiago-Alarcon *et al.*, 2008). Foxes on SMI had comparatively low prevalence values for ectoparasites. But for other parasites, SMI had some of the highest prevalence values of *Spirocerca* sp. and moderate values for a *Bartonella* bacterium compared with other Channel Islands (Namekata *et al.*, 2009; Coonan *et al.*, 2010).

In our present study, we recognize that the distribution of parasites and the resultant among host population variation in parasite assemblages may be attributed to any of a number of abiotic and biotic determinants. Much is known about the ecological, historical and environmental attributes of the Channel Islands (e.g. Moody, 2000; Orrock *et al.*, 2011) and the ecology of its inhabitants including the island fox. In particular, island fox populations differ in colonization histories, fox densities, recovery efforts and alternative host diversity. Foxes on both SMI and SRI were removed from the wild in the late 1990s and placed into a captive breeding

program to mitigate substantial predation from a novel, exotic aerial predator, the golden eagle (*Aquila chrysaetos*; Roemer *et al.*, 2002). Foxes on SCAT, a recently transported population, located in the southern island cluster had moderate levels of ectoparasite diversity and prevalence, despite having the highest effective population sizes of all Channel Islands fox populations. In contrast, the northern older, naturally colonized population of foxes on SMI had both the lowest ectoparasite diversity and effective population size (Aguilar *et al.*, 2004).

Larger populations tend to host more parasites; therefore, variation in island fox density may partly explain the observed ectoparasite delimitations. The populations sampled in our study all exhibited precipitous declines in numbers, although the cause varied from disease to predation. Additional efforts are needed to explore the impact of host characteristics on parasite composition among populations. For example, one might expect a strong correlation between body size and parasite diversity. However, our results do not support this hypothesis because ectoparasite diversity was not highest on SCAT, where the largest island foxes reside (Moore and Collins, 1995). Because diversity is often correlated among different taxa, the presence of alternative hosts provides additional resources to sustain a more diverse assemblage of parasites. Following this logic, again SCAT would be expected to have the highest ectoparasite diversity, given the presence of alternative mammals including exotic species such as bison and elk.

### Conservation of populations and endemic species interactions

Our findings demonstrate that host populations can be unpredictably unique in their species interactions, a result with at least two important implications for conservation.

First, when interactions of a host species differ throughout its geographic range, they are, in effect, expressing different ecological phenotypes (Stone *et al.*, 2011). Whether these different phenotypes deserve independent conservation is a topic for further discussion. If one considers the ability of hosts to serve as umbrella or keystone species for parasites, the loss of a host population that maintains two ectoparasite species (SMI) and one that maintains seven species (SRI) results in differential consequences on biodiversity due to the number of species connections (see network theory and coextinction literature – e.g. Colwell *et al.*, 2012). And because the persistence of species is dependent upon maintaining multiple populations, identifying these unique associations can aid in identifying conservation priorities and mitigating future threats.

Second, host populations with different parasites are likely to experience divergent selection pressures, resulting in different vulnerabilities to persistence (Thompson, 1996; Rigaud *et al.*, 2010). Clear examples exist in which regional differences in parasite faunas are associated with regional differences in selection. For example, stickleback populations in

northern Germany exposed to a wider array of internal parasites including cestodes and microsporidia were more diverse in their major histocompatibility complex (MHC) class genes – a suite of genes influencing parasite resistance through an adaptive immune response (Wegner *et al.*, 2003). We suspect that regional differences in parasite faunas and the selective pressures they impose may be common, particularly in isolated populations such as these island foxes. The resultant variations in host–parasite interactions could then generate novel evolutionary trajectories among host populations (Thompson, 1999). It is interesting to note, in this regard, that high levels of diversity in MHC were observed in San Nicholas Island foxes (not sampled in our study), a population that has fluctuated markedly over time and went through an extreme bottleneck, perhaps due to the influence of canine distemper virus and other canine pathogens (Aguilar *et al.*, 2004).

One might imagine the progressive transformation of the field of conservation biology from a species-centric view to a more process-based model, where maintaining interactions is the metric of recovery or restoration success (Thompson, 1996; Forup *et al.*, 2008; Tylianakis *et al.*, 2010). One intermediate step closer to considering not just species but interactions would be to evaluate the conservation value of species based on their number of connections with other species (i.e. ecological value). Theoretical work suggests that losing species for which many species depend is more likely to compromise the architecture, stability and function of ecological networks, and potentially lead to coextinctions (Dunne *et al.*, 2002; Koh *et al.*, 2004; Tylianakis *et al.*, 2010; Moir *et al.*, 2011; Colwell *et al.*, 2012). But more simply, hosts with different parasite interactions are, because of those interactions, different from each other in their ecological consequences. If the goal of conservation is, in large part, to conserve the roles of species, then conserving populations that differ in their interaction phenotype seems important. Recognizing the value of such interactions would require a broader acceptance of the value of parasites, given the acknowledged reality that most species on Earth are parasites and that parasites appear to have influence (in their presence or absence) on genetic-, population- and even ecosystem-level processes (Hudson *et al.*, 2006; Dunn *et al.*, 2009; Cardoso *et al.*, 2011).

In conclusion, as our results make clear, the presence of suitable hosts is required, but does not guarantee the occurrence of affiliated parasites (Moir *et al.*, 2011). But where host and parasite are both present, unique associations may emerge. In the case of the island fox, a species that is both endangered and endemic, the unique species interactions they harbour may be lost with their extirpation, and this consequence warrants more attention from the conservation community. It is naïve to assume no consequence of losing such interactions. Much research has focused on mapping the distribution of endangered and endemic species (e.g. Grenyer *et al.*, 2006). As the number of research projects studying the geographic distribution of some species of interest increases, implicitly our under-

standing about other species also improves because those species are likely either promoting or mimicking the same patterns. It is now necessary to explicitly determine the geographic distributions of rare and significant ecological interactions; see Real *et al.* (2009) for such an example. As the disciplines of conservation biology and biogeography continue to merge (Whittaker *et al.*, 2005), and we expand our traditional single species concepts to encompass species interactions (Araujo & Luoto, 2007), it is perhaps also necessary to redefine metrics of conservation success. In revisiting Thompson's (1999) plea calling for greater conservation of interaction diversity, we too advocate efforts that maintain ecological relationships to ensure that promoting processes in our environment remain.

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## BIOSKETCH

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Author contributions: N.C.H. and R.R.D. conceived the study. N.C.H. identified parasites, collected and analysed empirical data and wrote manuscript. T.J.C. and J.L.K. captured study species and provided field support. All authors contributed to edits and revisions.

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